Notes on the Origin, History, and Genetic Nature of the Cayenne Pineapple[1]

J. L. COLLINS[2]

ALTHOUGH PLANTS AND FRUITS of the pineapple had been carried from America to Europe a number of times following their discovery by Columbus in 1493, it was almost 100 years before they were successfully grown in Europe. They were first grown to fruiting in Holland about 1690 and in England some 30 years later, following the development of artificial heating of glasshouses.

Thereafter, a great rivalry and enthusiasm developed in the growing of pineapples by the gardeners of the large estates in England and on the continent. They imported varieties from America, exchanged varieties among themselves, and in some instances developed new varieties by growing the seeds which were occasionally found in their fruits or were obtained from the West Indies. As a consequence of this general interest in the growing of pineapples, the horticultural journals of the times frequently carried articles or notices concerning the culture of this fruit.

Like a number of important agricultural crops, the Cayenne variety of the pineapple, *Ananas comosus* (L.) Merr., appeared upon the horticultural scene with no definite record of the manner or the place of its origin. The first reference in the literature to the Cayenne variety appears to be the short notice carried in the *Gardeners' Chronicle* (England) of March 6, 1841, under the column heading of "Foreign Correspondence," as follows:

Paris, Feb. 4, 1841. As information is continually demanded by horticulturists regarding pines, perhaps a few words as to the varieties in request in Paris and the mode of culture may not be unacceptable. The Potager, or Royal Kitchen Garden Versailles has the merit of producing this and other fruits in the greatest perfection. . . . The pinery consists of a vast number of pits, succession and fruiting houses, the whole of which are heated with hot water; it contains about 2000 plants among which are fine specimens of Queens, Cayenne Lisse and Espineux, Black Jamaica . . . in all about 40 varieties. Only four kinds are considered desirable for general cultivation; of these, however, more than 1000 plants are annually fruited, namely 700 Queens and 300 Cayennes, Endville, and Providence. The Cayenne, both smooth and prickly, is of an excellent flavor and weight on the average from 9 to 12 pounds.

This article continues to record the names of the three principal growers, or nurserymen, for the French market, one each in Paris, Versailles, and Meridon, who list Cayenne plants along with some other varieties.

From this date, 1841, we trace the history of the Cayenne variety and map its distribution in geography and time.

In this first reference to the Cayenne variety, mention is made of the smooth-leaved and spiny-leaved forms. Genetic studies in Hawaii (Collins, 1936: 467) have shown that the smooth-leaved type infrequently produces spiny leaves; if we can judge from this modern behavior, then we can assume that the original Cayenne variety had smooth-edged leaves and also produced mutations giving rise to the spiny-leaved form as bud sports.

[1]Published with the approval of the Director as Miscellaneous Paper No. 48 of the Pineapple Research Institute of Hawaii, Honolulu, Hawaii. Manuscript received August 23, 1950.

[2]Department of Genetics, Pineapple Research Institute of Hawaii.

In the *Gardeners' Chronicle* for January 6, 1844, we find another reference to Cayenne in the section on "Notices to Correspondents," as follows: "The Cayenne pine is from French Guiana; cannot state its price, that is the affair of the nurseryman. . . ." A reader of this journal had obviously written to the editor inquiring about the place of origin of Cayenne and the price of plants, and the editor's reply indicates that it had been imported from French Guiana.

In a description of the Cayenne variety in "The Pineapple Manual" (Anonymous, *ca.* 1870), we find the statement that "This fine variety was imported from Cayenne many years ago and is now cultivated in many places."

These scattered and brief references, together with whatever weight may be given because of the name it bears, point rather clearly to Cayenne in French Guiana as the place from which this variety was introduced into France some time before 1840.

The fact that three French nurserymen in 1841 had sufficient material to offer Cayenne plants in their catalogues indicates its presence in France for a number of years previous to that date. In the "Pineapple Manual" mentioned above, the statement is made that "Cayenne is not very free in producing suckers." At the present time we consider that healthy plants will produce an average of about four reproductive shoots each in a 2-year growth period. The rate of increase from a small beginning would be very slow and could well require 15 or more years to produce enough plants so that three nurserymen could offer them for sale. Accordingly we may assume that a few plants may have reached France around 1820 to 1825.

MIGRATIONS OF THE CAYENNE VARIETY

With the distribution of plants to nurserymen in France, Cayenne soon became a favored variety in Europe because of its large, well-shaped fruits, good color, and fine flavor, although the Queen variety was also widely grown and well received. The earlier distribution of Cayenne to other countries appears to have stemmed from England and not directly from France. This early distribution from England is also emphasized by its early appearance in some of the British colonies, it having reached Australia by 1858 and Jamaica in 1870, although it came to Jamaica via Florida. In Australia its development was fairly rapid and from 1890 to 1895 that country was able to furnish many slips and suckers for expanding the pineapple industry in the Hawaiian Islands, although the first Cayennes came to Hawaii from Florida in 1885 and Jamaica in 1886.

The decade from 1885 to 1895 was a period of accumulation of the Cayenne variety in the Hawaiian Islands. Introductions of pineapple plants were made from 11 different tropical countries (Florida, England, Jamaica, Bahamas, Trinidad, Puerto Rico, Mexico, Australia, Singapore, Samoa, and Algeria) four of which were known to have included the Cayenne variety. It is possible that it may have been included in shipments from other countries as well, but the records do not list the varieties in some importations (Collins, 1934: 129).

Figure 1 shows two major centers of distribution of the Cayenne variety to other areas. England played this role during the last half of the nineteenth century, although the first European propagation was accomplished in France. Hawaii has been a major source of distribution during the first half of the twentieth century. It was doubtless sent to still other countries from these three major centers of distribution, but at present we do not have complete records. For instance, it was imported from Ceylon into South Africa, but we do not know how it reached Ceylon.

THE ORIGIN OF CAYENNE

The discussion of the Cayenne variety up to this point is based upon documentary evidence. In trying to trace the origin of the Cayenne pineapple beyond the realm of

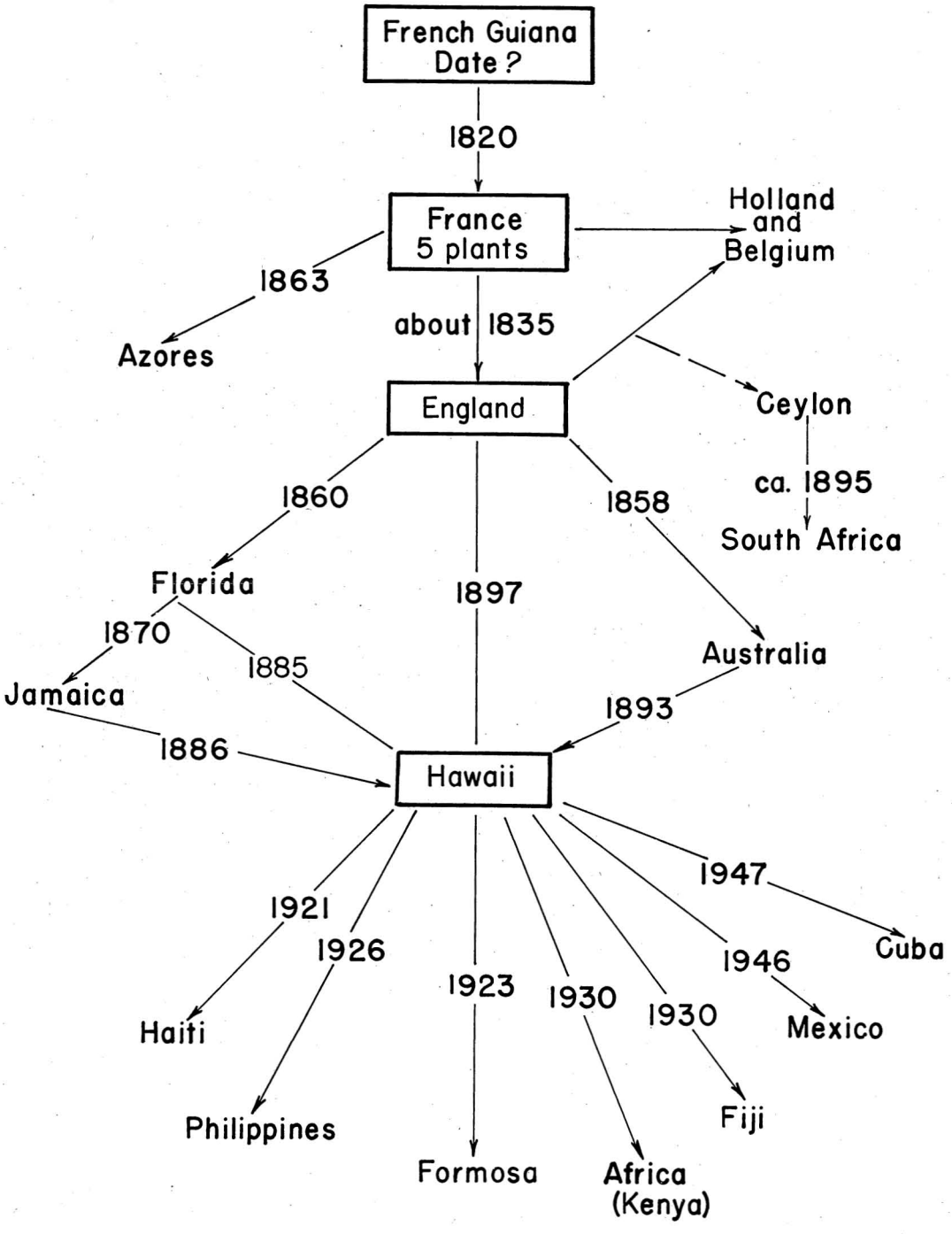

FIG. 1. Distribution of Cayenne following its introduction into France in 1820. Two major centers for distribution appear: first England and then Hawaii.

definitely known or documented history, certain additional conclusions regarding its still earlier history have been based upon circumstantial evidence.

As has already been stated, some of the early horticultural journals in England mentioned that the Cayenne variety had been imported from French Guiana. The name it bears is also circumstantial evidence for that conclusion. This latter statement is based upon the frequency with which plants, particularly the pineapple, are given names according to the place from which the varieties are obtained, even though they already possess local names. Among pineapples there are a number of varieties named after geographical areas in the West Indies and South America. Among these may be mentioned the following:

WEST INDIES	SOUTH AMERICA
Antigua	Bahia
Providence	Esmeralda
Jamaica	Pernambuco
St. Kitts	Taboga
Cuban	Surinam
Havannah	Trinidad
Puerto Rico	Demerara

In the hope that further knowledge regarding the history of the Cayenne variety might be found in French Guiana, a search was made of the botanical literature for reports of plants and plant collections in the northern part of South America. This search disclosed the information that in 1819 the French government sent an expedition to the French colonial possessions in America and the Pacific Ocean area to collect plants and seeds for the French botanical gardens at Paris and Versailles. Samuel Perrottet, the botanist on this expedition, filed a report of the plants collected, in which he records finding a new variety of pineapple growing at Cayenne, in French Guiana, having spineless leaves (the others in the region having spiny leaves) and delicately flavored fruits averaging about 20 pounds in weight (Perrottet, 1825: 103).

He collected and sent to Versailles five plants of this variety in 1820. This date fits in well with that which we have suggested above as being about the time the Cayenne variety is presumed to have been introduced into France.

The description, as it appeared in Perrottet's report, is included here as a part of the history of this variety, with a free translation following it.

Bromelia mai-pouri. Perr. Cette nouvelle espèce d'*ananas* provident de Cayenne; cinq plantes ont été, comme je l'ai dit déposés au jardin des primeurs à Versailles. Le mai-pouri n'a point les feuilles armées de dents comme ses congénères; ses fruits, d'un manger fort délicat, pèsent d'ordinaire 10 kilogrammes (20 livres), et sont très-beaux. M.

This new species of *Ananas* was procured from Cayenne; there were five plants as I have said, deposited in the garden of new varieties at Versailles. The mai-pouri does not have spiny leaves like its relatives; its fruits, of a very delicate flavor, weigh on an average 10 kilograms (20 pounds) and are very fine.

The description given by Perrottet is in itself not sufficient to establish the identity of "*Bromelia mai-pouri*" and the Cayenne variety. In fact, the 20-pound *average* weight of fruit mentioned by Perrottet is difficult to believe of any variety of pineapple and must represent an error in the record. The varieties Trinidad and Cabezona were reported to have fruits sometimes reaching 20 to 24 pounds, but there is no other reference to a variety having an average fruit weight anywhere near 20 pounds.

In commenting upon this description of *Bromelia mai-pouri*, Dr. L. B. Smith, of the National Museum in Washington, D. C., remarked that it looked as if someone made a major error between collection and publication. An inquiry concerning these plants sent to the Natural History Museum in Paris resulted in information that no herbarium specimens now existed of this Mai Pouri variety, but that they were considered the same as Smooth Cayenne in 1850 by Gautier, "the famous grower of Parisian pineapples." The

director of the museum stated that the duplication of names had been published, although the term "Mai Pouri" remains an unsupported name.

The supporting evidence of the date of its introduction into France and the postulated date based on the offering of plants for sale by nurserymen in 1841, together with the statement that Gautier believed the two to be identical in 1850, leads us to conclude that the five plants collected by Perrottet in 1820 represent the beginning of the Cayenne variety in France.

How did this variety get started in French Guiana? This question cannot now and perhaps may never be answered with certainty. The collection of five slips sent to France in 1820 we believe to be of the variety now known as Cayenne. Some time after it reached France it was given the name it now bears.

The name used by the French botanist in his report is somewhat confusing, since he calls it a new species of *Ananas*, yet listed it as *Bromelia*, a closely related genus in the pineapple family. However, Perrottet probably used the name given to him at the time he collected it. The name "Mai Pouri," by which this variety may have been known in French Guiana, probably followed the pattern of indicating the place from which it originated when it first appeared in French Guiana. The quest of the origin of the Cayenne was then continued in a search for a geographical area or locality having the name "Mai Pouri."

In Colombia, at the junction of the Triparro River with the Orinoco River, is a small village called "Maipures." In this region, and in the watershed of the Venturari River in Venezuela, also a tributary of the Orinoco, lived the Maipure tribe of Indians. We now believe that the Cayenne pineapple originated in the interior region of Venezuela long occupied by the Maipure tribe of Indians, and that it was probably grown and used by them for a long period of time (Fig. 2). Velez (1946: 427), who recently traveled through the upper Orinoco River basin, states that the Piaroa Indians have had under cultivation since time immemorial several pineapple varieties which yield large, well-flavored fruits.

Another circumstance which may also have a connection with Maipure pineapple concerns the Esmeralda pineapple variety, grown in Mexico. This variety is very similar, if not identical, to the Cayenne variety. Esmeraldas is the name of a small village at the mouth of the Esmeraldas River in northern Ecuador, in South America. The Maipure pineapple could have been carried from Venezuela or Colombia into the Esmeraldas region of Ecuador and thence into Mexico, where it was given the name of the place from which it had most recently come. We have no indication that it was known as Maipure while being grown in Ecuador, but there is good evidence that the Esmeralda and the Cayenne are the same variety.

How long had this variety been grown in the country of the Maipure Indians and why was it not found by Europeans at an earlier date? To the first question there is no definite answer. We suspect that the history of this variety may extend back into the antiquity of American civilizations along with such notable plants as corn, tobacco, and potatoes.

To the second question a logical answer is apparent. That area of South America is even today largely unexplored, partly because it has long been inhabited by Indians who have had little contact with outside people and because of the difficulty of travel in this little-frequented and still primitive area. The Maipure Indians, who at one time roamed over this area, no longer exist as a distinct ethnic group.

Sir Walter Raleigh, who conducted an expedition in 1595 up the Orinoco River for about 200 miles, reported having received quantities of pineapples from the Indians in the deep interior of the country. The village of Maipure on the Orinoco River is at the place now marked on maps as the head of navigation. This is some 200 miles farther up the Orinoco than the place reached by Ra-

leigh. Could Sir Walter Raleigh and his men have been the first white men to find and eat the Cayenne pineapple?

If the Cayenne pineapple originated in the Maipure Indian country, the parent variety or species may still be present as a part of the native vegetation. Other members of the hybrid population of which our Cayenne variety was a member may still be among those used by the Indians. Could some of the sibs of the Cayenne variety be better fitted for large-scale commercial production? Could some of the sibs have inherited resistance to diseases which Cayenne failed to obtain? Could some of the sisters of Cayenne have inherited two or more genes for yellow flesh color, where Cayenne obtained only one?

These are some of the questions which have been raised by this study of the origin of the Cayenne variety of pineapple, to which answers should sometime be obtained.

VARIATIONS WITHIN THE CAYENNE VARIETY

Two types of hereditary variations, which may be designated as strain differences and mutations, exist within the variety.

Strain differences

The term "strain" is used here to indicate hereditary differences in fruits or plants within a variety when the manner of origin of these differences is not known. A long time ago growers of this variety recognized strain differences. The *Journal of the Jamaica Agricultural Society* (about 1900) carried a statement that there was a good and a poor kind of Smooth Cayenne and that the latter was also known as the Honolulu kind!

Captain John Kidwell, an early pioneer of the pineapple industry in Hawaii, stated (Kidwell, 1904) that there were two distinct types in Hawaii, and that he considered one much superior to the other. The poor type of Cayenne, according to his statement, had been imported from Queensland, Australia, under the name of Smooth Cayenne. He described it as having a very large plant producing fruits weighing from 7 to 15 pounds and numerous slips on the peduncle beneath the fruit. The fruits, while of good quality, were conical in shape and possessed a very large core. The other type, which he called the "true" Cayenne, was similar in appearance, but the plants were smaller and produced fruits from 5 to 7 pounds in weight. This type did not produce slips on the peduncle beneath the fruit. As a consequence of this latter characteristic, this good strain was necessarily propagated from suckers and the crowns.

In 1887 a report of the United States Department of Agriculture on tropical and subtropical fruits mentions three kinds of Cayenne being grown in the Key West region of Florida. These were listed as Smooth Cayenne, Spine-leaved Cayenne, and Thompson's Smooth Cayenne. No description of the third kind was given, but its listing as a separate strain indicates that it may have been different in some respect from the others.

In Hawaii we recognize three strains of Cayenne, all of which produce good canning fruits but differ in some plant and fruit characters. The one used most extensively throughout the Islands is known simply as Cayenne. The second strain, grown mostly on Kauai, is known as the "Hilo" variety, or as the Hilo Cayenne. The Hilo variety differs from Cayenne in at least three characters. The most prominent difference is in the absence of slips in the Hilo variety. It also produces a smaller plant and fruit, with the fruit more cylindrical and of better average quality. It produces more suckers than Cayenne and the plants have a darker green leaf color. These differences are about the same as those Captain Kidwell used to distinguish between Cayenne and what he called the Queensland type. The strain we now call Hilo appears to

FIG. 2. Location of the probable area of origin of the Cayenne pineapple, showing the location of the town of Maipures on the Orinoco River. The Venturari River (Ven. R.) area, for a long time the country of the Maipure Indians, is also shown.

GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
Published by the University of Chicago Press, Chicago, Illinois
Copyright 1937 by the University of Chicago

TABLE 1
CLASSIFICATION OF SOMATIC MUTATIONS IN CAYENNE

FRUIT MUTATIONS

I. Foliar proliferation of the fruitlet
   1. Crowning Beauty
   2. Hour Glass
   3. Slipping Beauty
II. Multiplication of floral organs
   4. Flowering Beauty (increase in petal number)
   5. Multiple sepals and bracts
III. Disappearance of floral structures
   6. Dry fruit (only the floral bract subtending the fruitlet remains)
   7. Bottle Neck (the upper one half to one third of the fruit is like the dry fruit)
IV. Changes in fruit characters
   8. Elongated bracts and sepals
   9. Big eyes
   10. Slender
   11. Elongated fruit
   12. Self seedy
   13. Rough (pointed eyes)
   14. Non-porous flesh
   15. White flowers
   16. Nubbin (dwarf and abnormal fruit—eyes small and distorted, surface very rough) M226

PLANT MUTATIONS

V. Single character changes
   17. Spiny leaves
   18. Absence of anthocyanin
   19. Linear anthocyanin
   20. Blush anthocyanin
   21. Intensified anthocyanin
   22. Albino (no chlorophyll)
   23. Streaked anthocyanin
   24. Waxy (absence of trichomes)
   25. Semi-waxy (reduction in trichomes)
   26. Mealy (increased trichomes)
   27. Few slips (573, M4W)
   28. Increased number of slips (L69)
   29. Multiple crowns
   30. Increased wilt tolerance (resistance)
   31. Increased chlorophyll (LH8)
VI. Multiple character changes
   32. Paper Leaf (degenerate plant)
   33. B.B. (gigas form)
   34. Lanai (short leaf type)
   35. Driver's Dwarf (dwarf)

be identical with the one Kidwell called the "true" Cayenne.

Our third strain is known as the Collar-of-Slips, because of the excessive number of slips produced around the base of the fruit. It has a smaller fruit than the Hilo, is later in maturing its plant and ratoon crops, and is generally considered an undesirable type.

These Cayenne strains have been present as components of the variety for a long, long time. How they originated or which represents the true or original Cayenne cannot now be determined with certainty.

FIG. 3. A plant of the Cayenne variety, showing slips, suckers, and a mature fruit.

Figure 3 shows a typical Cayenne plant with slips, suckers, and a mature fruit.

Mutations

The term "mutation" is applied to new hereditary variations which appear *de novo* in a population of plants or animals, caused by a change in the structure of a chromosome and thus in the hereditary constitution of the individual.

Mutations have occurred in the Cayenne variety, giving rise to a series of new or changed forms; some are so profoundly changed that they no longer show the variety characters, others show only minute changes.

These mutant forms are treated separately from the strains already discussed, principally because we know something about the origin of these mutations and we do not know how the strains originated. It is quite possible that the latter also started as somatic mutations.

The mutations in Cayenne can be conveniently divided into six classes on the basis

of the characters which are altered. Four classes affect the fruit and two classes affect both fruit and plant characters (Table 1).

The mutations listed in the first five classes of Table 1 are relatively slight or small character alterations. They influence one or a few characters and do not, for the most part, represent profound genetic changes, even though the character alteration may be conspicuous. The mutant Crowning Beauty (Fig. 4) is an example of this kind of mutation.

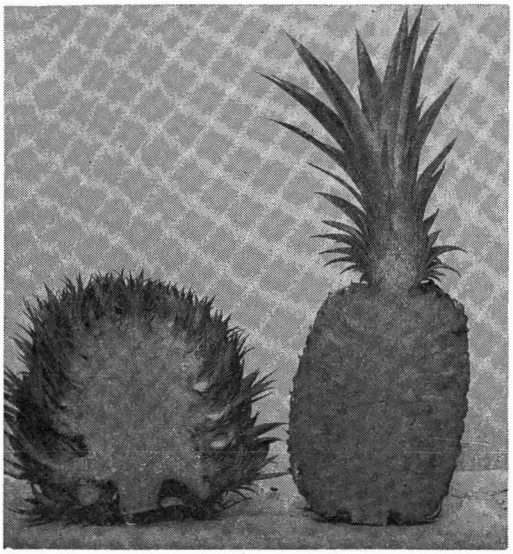

FIG. 4. A normal Cayenne fruit cut in longitudinal section on the right, showing internal structures of core, carpels, and vascular fibers. On the left is the mutant type Crowning Beauty, showing foliar proliferation of the fruitlets and absence of normal carpel structures.

Those in Class VI, however, stand apart from the rest because they represent simultaneous changes in a number of different morphological and physiological characters.

The Lanai type and B.B. mutations (Fig. 5) appear to be complementary to each other in their deviation from the normal variety. They vary from typical Cayenne in opposite directions in at least six characters, shown in Table 2.

TABLE 2
CHARACTERS OF MUTANTS B.B. AND LANAI COMPARED WITH THOSE OF THE NORMAL VARIETY

CHARACTER	VARIATION FROM TYPICAL CAYENNE	
	In B.B.	In Lanai
Leaf number.....	decreased	increased
Leaf length.....	increased	decreased
Fruit size.....	larger	smaller
Fruit maturity....	later	same as normal
Plant size.....	larger	smaller
Spines	more	normal

The Paper Leaf mutant departs so widely from the normal variety in a number of characters that it no longer resembles the Cay-

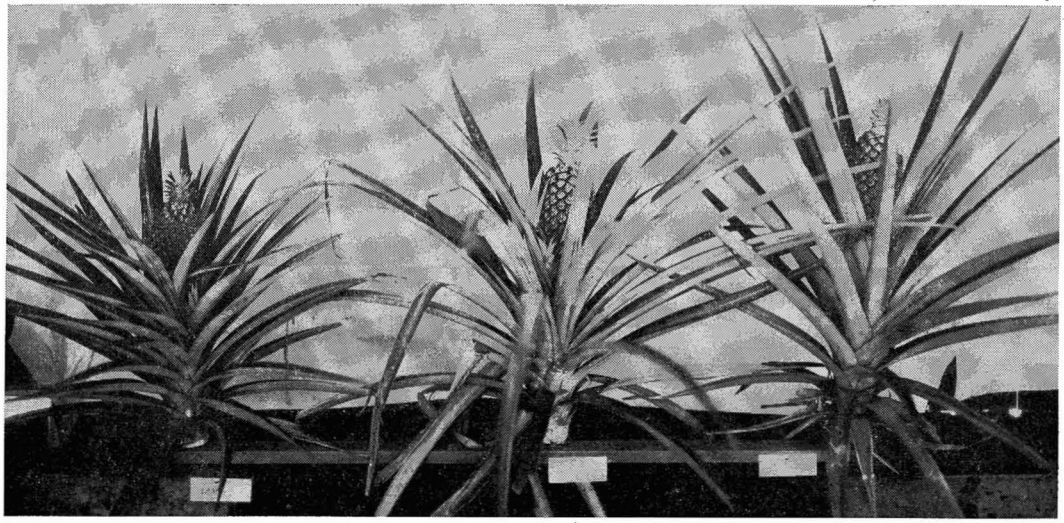

FIG. 5. A normal Cayenne plant in the center, with the short leaf Lanai mutation on the left and the long leaf one on the right. These represent changes in opposite directions from the normal.

enne at all. It is considered a degenerate type, because of its small, worthless fruit and weakly growing plant. It probably could not survive in field competition with normal plants.

Driver's Dwarf (Fig. 6) has a diminutive form of plant and fruit, combined with collar of slips and an intensified purple anthocyanin pigment in the leaves. This may represent a change from the normal slip type of the Cayenne variety to the collar-of-slip strain. On the other hand, the mutation giving rise to dwarf and increased anthocyanin may have occurred in a collar-of-slip strain plant which was already in the field population. The dwarfing and anthocyanin intensification appear to have been simultaneous changes.

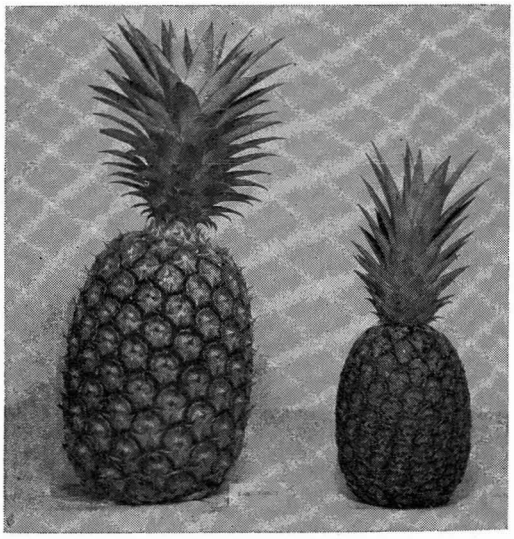

FIG. 6. A normal Cayenne fruit on the left, with a fruit of the mutant Driver's Dwarf on the right.

Discussion of these more obvious mutant types naturally leads to the question of the possible occurrence of other mutations which are less conspicuous and less easily measured. Undoubtedly mutations of this kind take place, but the demonstration of the existence of mutations of slight phenotypic effect is much more difficult, because of overlapping variations of a non-hereditary nature.

Some examples of these small or elusive mutant effects are briefly described to show that at least a few are present in the variety.

Two Cayenne clones were found to show a slightly darker green color, which could be recognized easily when a fairly large group of these were growing adjacent to a group of the normal variety. A clone may be thought of as one plant multiplied many times by vegetative reproduction, and all plants of a clone have identical heredity. Chemical analyses of leaves revealed a higher chlorophyll content in these darker green leaves. A mutation of slight effect on chlorophyll production was probably the origin of these darker green clones.

The elongated fruit mutation listed in Table 1 develops a large number of multiple crowns and fasciated fruits when grown in warm, dry areas, but only normal plants appear in the cool, more moist areas. In this case the additional character of multiple crowns is quite obvious under one environmental condition and disappears (or merges into the normal pattern) when grown under other conditions.

The number of slips produced per plant is a character subject to considerable variation due to differences in the environment during the growth period. This is well illustrated by the effect of relative crowding of plants in the field. Close planting reduces the number of slips, and, conversely, widely spaced plants permit a larger number of slips to develop. Table 3 shows the variation in number of slips resulting from an experimental planting of Cayenne with 10, 12, 14, and 16 inches between plants (that is, with different degrees of crowding).

TABLE 3

EFFECT OF DIFFERENT PLANT SPACINGS ON SLIP PRODUCTION

PLANT SPACING IN INCHES	AVERAGE NUMBER OF SLIPS
10	2.51
12	3.33
14	3.95
16	4.36
Odds — 19 to 1	0.43
Odds — 99 to 1	0.60

Because of the susceptibility of this character to variation due to environmental dif-

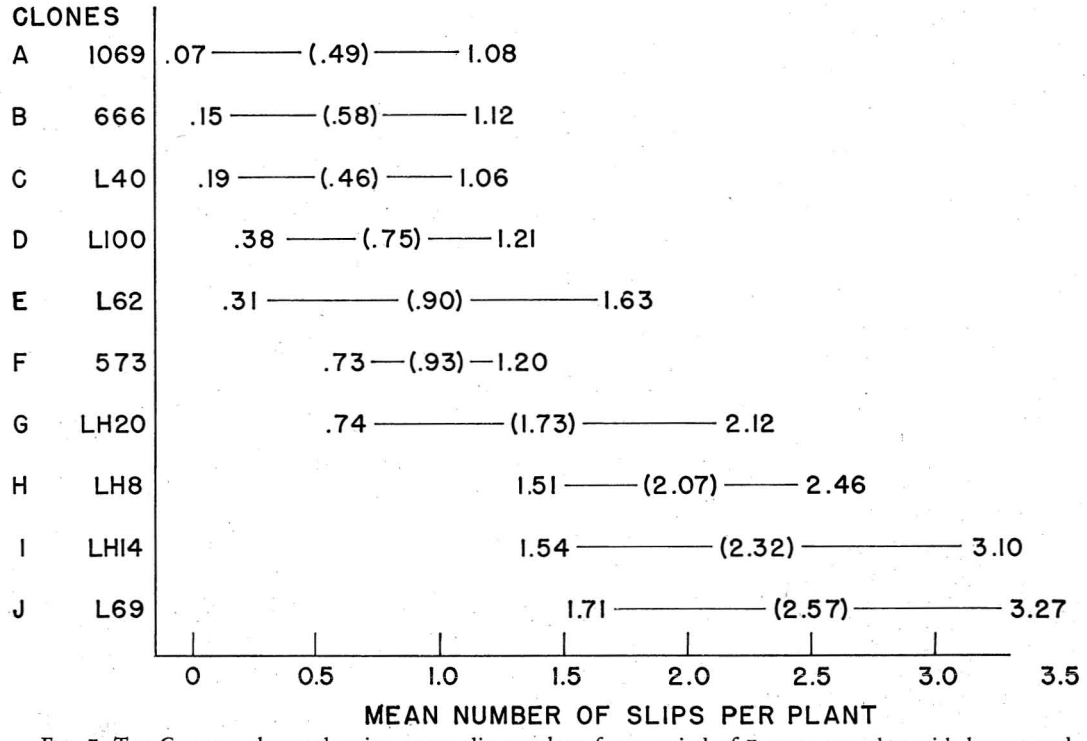

FIG. 7. Ten Cayenne clones showing mean slip numbers for a period of 7 years, together with lowest and highest yearly means.

ferences, the discovery of genetic variations (somatic mutations) which have an effect on slip number is more difficult than locating mutations which are not subject to environmental modification. However, by repeated tests under similar environmental conditions it has been possible to demonstrate the occurrence of mutations affecting number of slips in this variety.

Figure 7 shows the mean number of slips per plant for 10 clones over a period of seven plant crop harvests, together with lowest and highest limits of the yearly means for that period. Five of the clones had a range of annual mean slip number which did not overlap the range of three other clones. Two clones, E and G, had a range of variation which overlapped all the other groups. There can be little doubt about a genetic difference existing between any one of the three high slip-producing clones, H, I, J, and any one of the five low-producing clones, A, B, C, D, and F.

The three high slip-producers, H, I, and J, do not appear[3] to differ among themselves. Clone G, overlapping in its range with both the high and low slip producers, appears to be genetically different from both groups.

These mutant clones can be compared with each other, but should not be compared with the mean of the variety, first because they are a part of the variety and second because—the variety being a mixture of genetic types—random samples would not always include the same distribution of variant types. Furthermore, most Cayenne populations include some plants of the collar-of-slip strain, which produces a very high number of slips.

The somatic mutations in Cayenne include a range of types varying from those having

[3]These conclusions are based upon another replicated plot test which showed significant differences as listed here, and we presume that the causes of the differences were genetic.

marked, easily recognized characters to those differing so slightly that only statistical analyses of quantitative data will identify them.

They are not frequent in occurrence, with the exception of a few which have been shown to be frequently mutating types (Collins, 1936). The mutations discussed here have been collected over a period of 20 years or more and from among millions of normal plants.

This variety is as stable genetically as are vegetatively propagated, highly heterozygous diploid varieties in general. Were this not true, the variety could not have been maintained through this long period of time.

Cayenne is not the single clone it probably was at the beginning. Now it is a collection of clones, all having the same general characters but usually differing in one or a few characters or degrees of expression of characters. The more obvious mutations and those too poorly adapted to survive in the general population have been and are being reduced to small percentages or eliminated. The remaining population heterozygosity consists of minor character alterations which are carried along by asexual propagation in the general mass of cultivated plants. As examples of these latter clonal types, reference can be made to some of those listed in Table 1, such as the clone with less porous fruits, self-seedy types, low and high slip-producing forms, and increased amount of chlorophyll.

As to their value to the organism (in a cultivated variety, positive value in horticulture) these somatic mutations follow the known pattern of randomly occurring mutations; the great majority are either detrimental or of no advantage to the organism. Only three of those which have been studied appear to have possible advantage in pineapple culture, and only two of these, the wilt-resistant mutant and the high slip-producing type, are of possible importance.

TETRAPLOID CAYENNE

The pineapple normally has 50 chromosomes in its somatic cells. This is considered to be the diploid number for the genus *Ananas*. However, tetraploid Cayenne plants having 100 chromosomes were obtained after treating shoot growing points with colchicine solution (Kerns and Collins, 1947). The immediate results from these treatments were various kinds of chimeras of diploid and tetraploid tissues, together with plants which either died early in growth or reverted to normal diploid tissue throughout.

By careful selection of buds from the tetraploid sectors of chimeras during several successive vegetative generations, constant new types which fall into the following three classes on the basis of the amount and location of tetraploid tissue were obtained.

Class 1 was completely tetraploid.

Class 2 was tetraploid except for a diploid epidermis.

Class 3 was diploid except for a tetraploid epidermis.

Classes 1 and 2 were alike in all visible characters. Class 3 was like the normal diploid in all visible characters.

The tetraploid has been compared in Table 4 with the diploid in a number of important characters. The fruit weight is less in the tetraploid and the fruit has fewer eyes than in the diploid. The average eye weight, however, is higher in the tetraploid, showing that the individual eyes of the tetraploid are larger. The Brix (dissolved solids including sugars) of the tetraploid fruit is lower than in the diploid fruit. The characters of fruit acidity, translucence, and vitamin C content are highly variable, so that no significant differences were obtained. These characters are readily altered by different environmental conditions.

Tetraploid plants are taller than diploids, but they have fewer leaves and produce fewer slips. They do not differ in average leaf length, although the tetraploids have wider leaves. The tetraploids also have a higher percentage of water in the leaves and, as a consequence, a lower percentage of dry matter per unit weight of green leaf tissue.

The fruits are seedless, as are the diploids. The chromosomes perform regularly in germ-cell formation, and functional gametes are produced.

Crosses between the Cayenne tetraploid and varietal hybrid tetraploids produce viable seed readily, but crossing with diploid forms produces very little seed; this is similar to the results obtained when varietal hybrid tetraploids are crossed with diploids.

TABLE 4

COMPARISON OF THE FRUIT AND PLANT CHARACTERS IN THE DIPLOID AND TETRAPLOID CAYENNE

CHARACTERS	DIPLOID	TETRAPLOID
Fruit weight (lbs.)	5.8	4.0*
Eye number	140.4	105.6*
Eye weight (gm.)	16.3	16.8*
Brix	15.4	13.8*
Acidity (per cent)	0.71	0.86
Vitamin C	19.2	20.8
Translucence	2.7	2.3
Plant height (cm.)	28.1	30.5*
Number of active leaves	57.6	44.2*
Leaf length (cm.)	65.0	65.2
Leaf width (cm.)	5.4	6.2*
Percentage water in leaves	81.8	83.5*
Percentage dry matter in leaves	18.2	16.5*
Pollen grain diameter (microns)	47.0	64.0*
Stomata size (microns)	22.0	31.0*

*Significant differences.

In many plants, and particularly in ornamentals, valuable horticultural characters are obtained by doubling of the chromosomes (Emsweller, 1948: 570). However, the tetraploid Cayenne is inferior to the diploid form in several important characters (Table 4).

GENETIC NATURE OF CAYENNE

The Cayenne pineapple normally has seedless fruits, although it does produce normal germ cells. The seedlessness results from a condition known as self-incompatibility. Under these conditions the germ, or sex, cells of the same individual do not unite in fertilization to form embryos. Germ cells from two different varieties, Cayenne and Queen, for instance, are mutually compatible and seeds are produced following cross pollination between the varieties.

Inasmuch as inbreeding is thus denied because of self-incompatibility, the studies of the genetic nature of Cayenne have been conducted largely from the results of varietal crossings and from examination of the somatic mutations which have appeared in field populations.

Cayenne has a diploid number of 50 chromosomes; in the somatic cells they appear slightly elongated or almond-shaped (Collins and Kerns, 1931: 140); in the germ cells, they are almost round. While the process of germ-cell production is usually normal, some abnormalities occur. The most frequent abnormality is the formations of germ cells containing 50 chromosomes, which is double the ordinary number of chromosomes in gametes. These appear in the mature sex cells as giant pollen grains and ovules.

In crosses between Cayenne and other varieties, these giant germ cells give rise to occasional hybrids having 75 or 100 chromosomes instead of the normal number of 50 for this species.

The number of these plants whose cells have 75 and 100 chromosomes is far below the expected number on the basis of the percentage of 50-chromosome germ cells produced. This shows that only a small proportion of the plant gametes function in fertilization and that selective fertilization in favor of the normal 25-chromosome gametes takes place.

Hybrid populations resulting from crossing Cayenne with other varieties provide some information regarding the genotype or hereditary constitution of the Cayenne variety.

The variety is heterozygous for many recessive and dominant genes. Table 5 gives some information on the genotype of Cayenne obtained from crossing with other varieties.

INBREEDING IN CAYENNE

In discussing the somatic mutations which have appeared, mention was made of the self-

TABLE 5
THE GENOTYPE OF CAYENNE WITH RESPECT TO CERTAIN CHARACTERS

CAYENNE CHARACTER	CONTRASTING CHARACTER	CAYENNE GENOTYPE	CAYENNE DOMINANCE RELATION
Spiny tip leaves	spiny leaves	Ss	dominant
Spiny tip leaves	piping leaves	pp	recessive
Anthocyanin in leaves	no anthocyanin	Aa	intermediate
Yellow flesh	white flesh	Yy	intermediate
Purple petals	white petals	WW	dominant
Chlorophyll	no chlorophyll	Cc	dominant
Normal fruit	proliferation	*	recessive
Seedless	seedy	*	recessive
Long leaves	short leaves	*	dominant

*Undetermined.

fertile mutation. In this form, the self-incompatibility characteristic of Cayenne is replaced by self-fertility as a result of a dominant mutation, but in all other respects the variety characters remain unchanged.

Inbreeding can now be carried out in the variety by using these self-fertile mutants. Inbreeding is a potent tool for dragging recessive skeletons out of hereditary closets and displaying them in the light of day for all to see. By the use of this tool we have pried out of Cayenne recessive secrets which it has long carried buried within its genotype.

About one fourth of the inbred progeny are semi-lethal and die in an early seedling stage. Another fourth are so weak that they grow very slowly and reach fruiting maturity long after the parent Cayenne. Most of the inbreds are low in vigor, with only a few approaching that of the Cayenne variety. They exhibit a wide variation in fruit and plant types, including many fruit and crown fasciations. The inbred population supplies evidence that Cayenne is not only heterozygous for many recessive and some dominant characters, but that it exhibits heterosis or hybrid vigor.

A number of variations which had appeared in the variety as somatic mutations also appear in the inbred population in numbers indicating Mendelian segregation in a heterozygous genotype.

The general characteristics of the inbred populations supply some evidence regarding the parentage of Cayenne itself. The origin of this variety as a hybrid between any of the known species of *Ananas* can be ruled out, we believe. The parent or parents producing this variety through sexual reproduction must be considered at present as unknown varieties of *A. comosus*, or of such a variety of *A. comosus* and a species of pineapple not known at the present time.

SUMMARY

The Cayenne variety of pineapple was first mentioned in an English horticultural journal in 1841. Evidence is presented to show that it came from French Guiana in 1820. It is presumed to have been grown by the Maipure Indians in the upper Orinoco River valley long before it reached French Guiana. The manner and time of its origin are obscure.

After its introduction into France and England, it became established in many tropical countries during the 100 years between 1840 and 1940.

The genotype of the variety is highly heterozygous and it exhibits hybrid vigor in its growth. The variety is self-incompatible and must be propagated vegetatively. During its long period of vegetative propagation a number of somatic mutations have appeared, including one giving the mutant type self-compatibility. The present Cayenne is a miscellaneous collection of clones. The diploid chromosome number is 50, with 100-chro-

mosome tetraploids obtained by treatment of diploids with colchicine. The tetraploids are inferior to the diploids.

REFERENCES

ANONYMOUS. *Ca.* 1870. The pineapple manual, being a guide to the successful cultivation of the fruit and construction and management of the pinery by contributors to the Journal of Horticulture. London: *Jour. Hort. and College Gardener.*

COLLINS, J. L. 1934. Introduction of pineapple plants into Hawaii and some brief accounts of pioneer pineapple growing. *Pineapple Quart.* 4: 119–120.

——— 1936. A frequently mutating gene in the pineapple, *Ananas comosus* (L.) Merr. *Amer. Nat.* 70: 467–476.

——— and KENNETH R. KERNS. 1931. Genetic studies of the pineapple. I. A preliminary report upon the chromosome number and meiosis in seven pineapple varieties (*Ananas sativus* Lindl.) and *Bromelia Pinguin* L. *Jour. Hered.* 22: 139–142.

EMSWELLER, S. L. 1948. Breeding of ornamental plants. *Amer. Soc. Hort. Sci., Proc.* 51: 565–574.

KERNS, K. R., and J. L. COLLINS. 1947. Chimeras in the pineapple. *Jour. Hered.* 38: 323–330.

KIDWELL, CAPT. JOHN. 1904. The cultivation of pineapples in Hawaii. *Hawaii. Forester and Agr.* 1 (12).

PERROTTET, SAMUEL. 1825. Catalogue raisonné des plantes introduites don les colonies française de Mascareigne et de Cayenne, et de celles rapportées vivantes des mers d'Asie et de la Guyane au Jardin des Plantes de Paris. *Mem. Soc. Linn.* 3(3): 89–151.

VELEZ, ISHMAEL. 1946. Wild pineapples in Venezuela. *Science* 104: 427–428.